

OVEJECTOR STRUCTURE IN THE HAEMONCHINAE (NEMATODA:TRICHOSTRONGYLOIDEA) OF RUMINANTS

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ABSTRACT: The use of ovejector structure in the phylogeny of the Haemonchinae is hampered by differences among nematologists in the application of terminology and the recognition of homologous parts. Some workers recognize a sphincter with 2 parts, but others recognize only the proximal, rounded part of the sphincter and include the distal cylindrical part of the sphincter with the vestibule. The results of this study demonstrate that all sphincters of Haemonchinae of ruminants have 2 parts. To encourage the application of a uniform terminology to homologous parts of the ovejector, we propose the use of the terms “sphincter 1” for the rounded part and “sphincter 2” for the cylindrical part. It is hoped that clarification of the terminology for ovejectors of the Haemonchinae will provide a model useful for improving descriptions of ovejectors throughout the Trichostrongyloidea.

Species of Haemonchinae include some of the most important nematode parasites of domestic and wild ruminants. In the course of recent descriptions of several species of *Haemonchus* Cobb, 1898 and *Ashworthius* Le Roux, 1930 it became apparent that terminology for the parts of the ovejectors of these nematodes was not applied uniformly. The muscular ovejectors are a prominent feature of most female Strongylida. The comparative structure of ovejectors has been demonstrated to be useful in the systematics of the Strongyloidea (Lichtenfels, 1980; Beveridge, 1987). For comparative ovejector structure to be useful in phylogenetic studies of the Haemonchinae, and broader related groups, differences must be resolved in the recognition of homologous parts and the terminology applied to them. The terminology in current use universally employs the terms infundibulum, sphincter, and vestibule for the parts of the paired, muscular ovejectors (Chitwood and Chitwood, 1950), but the application of the terms to structural parts is inconsistent. In recent descriptions of species of *Haemonchus* and *Ashworthius*, some workers (Lichtenfels et al., 1994, 2001; Hoberg et al., 2002; Lichtenfels et al., 2002) followed the concept of Veglia (1915), which recognizes a sphincter with 2 parts, but others (Ferte and Durette-Desset, 1989; Giudici et al., 1999) followed the concept of Durette-Desset (1983), which recognizes only the proximal, rounded part of the sphincter and includes the distal cylindrical part of the sphincter with the vestibule.

Thus, for the Haemonchinae (as with most trichostrongyloid nematodes), there are 2 different interpretations of parts of ovejectors centered in the structure of the sphincter. The differing interpretations constitute a barrier to comparative morphology of the ovejector and its use in phylogenetic studies. The objective of the present study was the examination of the structure of ovejectors within the Haemonchinae, an economically important subfamily currently under systematic revision, in an attempt to recognize homologous parts and to recommend a uniform application of terminology for the parts. The results of this study may be useful also for comparative studies of ovejectors of other taxa of the Trichostrongyloidea and, potentially, for other groups within the Strongylida.

MATERIALS AND METHODS

The ovejectors of all 12 species of *Haemonchus*, 4 of 8 (all available) species of *Ashworthius*, and the single species of *Mecistocirrus* were studied (Table I). Most specimens were obtained from the U.S. National Parasite Collection, Beltsville Agricultural Research Center, Beltsville, Maryland.

Specimens were studied as temporary, wet, whole mounts, cleared in phenol–alcohol (80 parts melted phenol crystals and 20 parts absolute ethanol), or in cross sections cut at 6 μ m with a microtome after embedding in paraffin and staining with hematoxylin and eosin. Interference-contrast light microscopy was used to study the ovejectors at a magnification of $\times 200$ –400. Drawings were prepared with the aid of a camera lucida. Photomicrographs were obtained with 35-mm cameras using Kodak T-Max 100 black and white film or Kodak Ektachrome 64T. Selected images on film were digitized with a Nikon Cool Scan III. Photomicrographs were prepared for presentation in Microsoft PowerPoint. Measurements were made with a calibrated ocular micrometer.

We follow the classification of the Trichostrongyloidea provided in the *CIH Keys to Nematode Parasites of Vertebrates*, No. 10 (Durette-Desset, 1983) rather than the more restricted definitions provided by Durette-Desset and Chabaud (1993) and Durette-Desset et al. (1999) for reasons stated previously (Lichtenfels and Pilitt, 2000).

RESULTS

The structure of ovejectors of 12 species of *Haemonchus* (Figs. 1–19) was found to be remarkably uniform. All 12 species exhibited opposed paired ovejectors joined by a common vestibule, with anterior and posterior branches, each consisting of a cylindrical, thickly muscled sphincter of 2 parts, and an elongate infundibulum. The most notable difference among the ovejectors of the 12 species was the bilobed structure of the vestibule of *H. lawrencei* (Figs. 4, 14). The ends of all 3 parts of the ovejectors are marked at their junctions by distinct constrictions and a discontinuity of muscle and lining cell layers (Figs. 1, 13–15). Nuclei of the cells lining the muscular ovejectors were usually not visible in the available specimens, and no attempt was made to count the cells lining the parts of the ovejectors.

A detailed drawing of the ovejector of *H. placei* (Fig. 1) and photomicrographs of ovejectors in cleared whole mounts of *H. dinniki* (Fig. 13), *H. lawrencei* (Fig. 14), *H. contortus* (Fig. 15), and *H. similis* (Fig. 16) and in histological cross sections of *H. similis* (Figs. 17–19) show the muscle and cellular layers typical of all the species (Sachs et al., 1973; Lichtenfels et al., 1994). All other drawings show only the size and shape of the 3 parts in outline.

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TABLE I. List of specimens studied.

	Collection Nos.*	Host/Locality
Species of <i>Haemonchus</i> Cobb, 1898		
<i>H. contortus</i> (Rudolphi, 1803) Cobb, 1898	70001	<i>Ovis aries</i> /Georgia
	70374	<i>Bos taurus</i> /Maryland
<i>H. longistipes</i> Railliet & Henry, 1909	92573	<i>Camelus dromedarius</i> /Sudan
<i>H. placei</i> (Place, 1893) Ransom, 1911	70372, 70382	<i>Bos taurus</i> /Florida, Louisiana
<i>H. similis</i> Travassos, 1914	39902, 70301	<i>Bos taurus</i> /Florida
<i>H. bedfordi</i> Le Roux, 1929	1998.11.19.2–6*†	<i>Connochaetes taurinus</i> /Natal, South Africa
<i>H. mitchelli</i> Le Roux, 1929	1998.11.19.27–41†‡	<i>Taurotragus oryx</i> /Natal, South Africa
<i>H. vegliai</i> Le Roux, 1929	87598	<i>Tragelaphus angasii</i> /South Africa
<i>H. lawrencei</i> Sandground, 1933	76044‡	<i>Cephalophus monticola</i> /South Africa
<i>H. okapiae</i> van den Berghe, 1937	61420‡	<i>Okapia johnstoni</i> /Zaire
<i>H. krugeri</i> Ortlepp, 1964	87596	"Impala"/South Africa
<i>H. dinniki</i> Sachs, Gibbons & Lweno, 1973	1998.11.19.14–23†	<i>Rhynchotragus kirkii</i> /Tanzania
<i>H. horaki</i> Lichtenfels, Pilitt, Gibbons & Boomker, 2001	70277‡	<i>Pelea capreolus</i> /South Africa
Species of <i>Ashworthius</i> Le Roux, 1930		
<i>A. pattoni</i> Le Roux, 1930		Literature only
<i>A. sidemi</i> Schulz, 1933	89169	<i>Cervus elaphus sibiricus</i> /Russia
<i>A. martinagliai</i> Ortlepp, 1935		Literature only
<i>A. leporis</i> Yen, 1961	Not studied	
<i>A. lerouxi</i> Diaoure, 1964	66647	<i>Syncerus caffer</i> /Uganda
<i>A. tuyenquangi</i> Drozd, 1970	91946‡	<i>Muntiacus muntjak</i> /Vietnam
<i>A. perrilli</i> Chauhan, Pande & Singh, 1972		Literature only
<i>A. patriciapilittae</i> Hoberg, Abrams, Carreno & Lichtenfels, 2002	90048, 90049, 90050‡	<i>Odocoileus virginianus truei</i> /Costa Rica
Species of <i>Mecistocirrus</i> Railliet & Henry, 1912		
<i>M. digitatus</i> (Linstow, 1906) Railliet & Henry, 1912	58397	<i>Bos taurus</i> /Panama
	86686	<i>Bos indicus</i> /Philippines
	88290	<i>Bos indicus</i> /Thailand

* U.S. National Parasite Collection unless indicated otherwise.

† British Museum of Natural History.

‡ Type specimens.

The infundibulum, the most proximal part of the ovejector, communicates with the thin-walled uterus, and its narrow distal end is surrounded by the rounded, proximal part of the sphincter. The infundibulum has the thinnest muscle layer of the 3 parts of the ovejector, and its muscle fibers are distributed in a circular pattern around the lumen (Figs. 1, 18). The cells lining the lumen of the infundibulum are thicker than the muscle layer, and they have longitudinal ridges that line the lumen (Figs. 1, 18). The infundibula are the longest parts of the ovejectors.

The 2-part sphincter is the middle part of each of the paired ovejectors, and it has the thickest muscle layer (Figs. 1, 13–17). The muscle fibers in the rounded proximal part are arranged in a spiral pattern that is more transverse than in the rest of the sphincter. The cylindrical second part of the sphincter is set off from the rounded proximal part by a slight constriction, and it has a slightly thinner, more uniform muscle layer (Figs. 1–16). The muscle fibers of the cylindrical part of the sphincter are only slightly spiral, almost parallel with the lumen. Both parts of the sphincter are covered by a fluffy coat consisting of sarcoplasm and muscle cell nuclei. The lumen of the sphincter is lined with a cellular layer with a thick, convoluted surface (Figs. 1, 13–17). The junctions of the sphincters with the vestibules are marked by a constriction and discontinuities in muscle and cellular layers of these parts.

The vestibule of *Haemonchus* spp. is kidney-shaped to cylin-

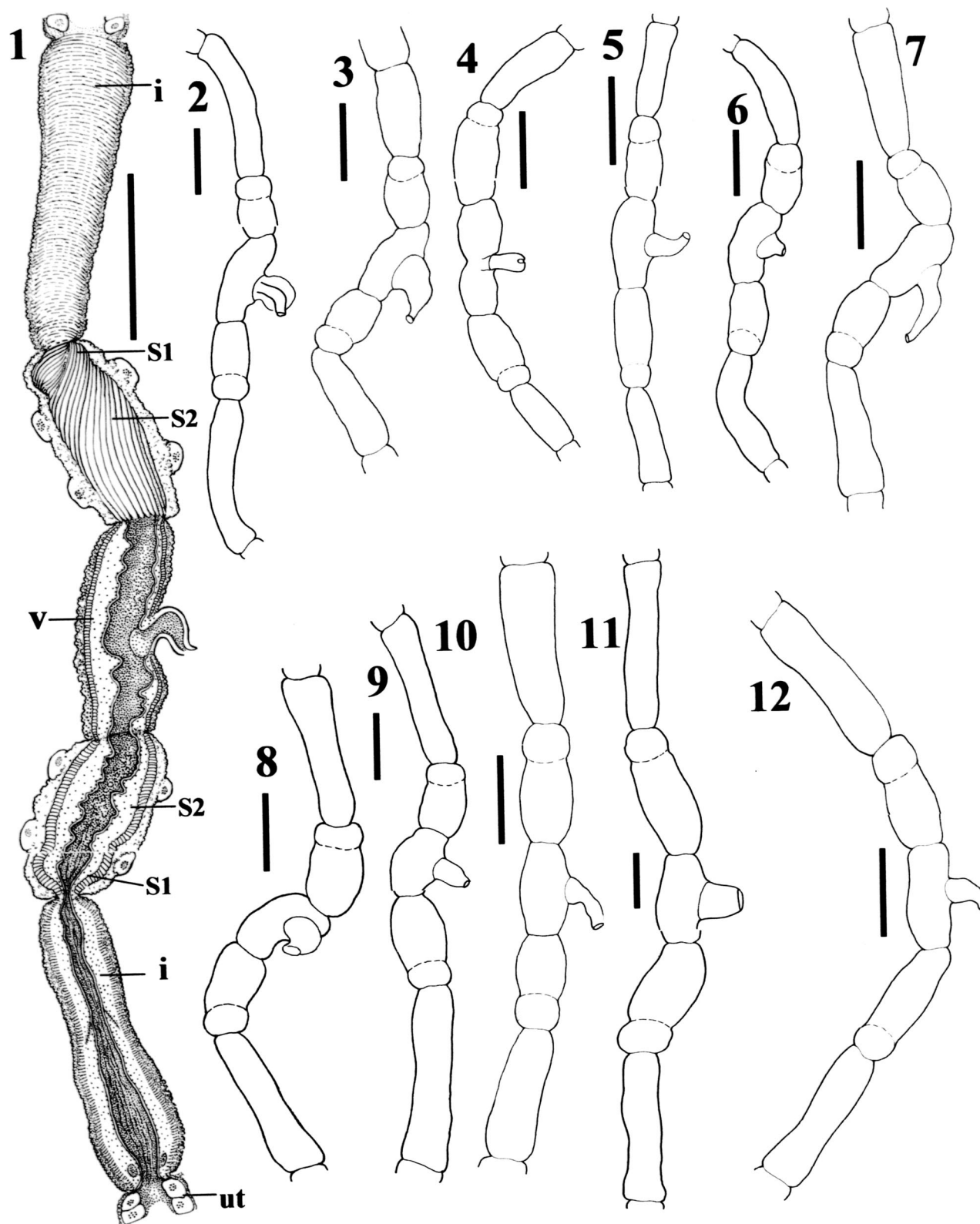
drical and may be slightly longer or shorter than one of the paired sphincters. The muscle fiber and fluffy coat layers are each thinner in the wall of the vestibule than in the sphincter. The cellular lining of the vestibule is thicker but less convoluted than in the sphincter. The vagina, with its thick cuticular lining, joins the vestibule midventrally.

The ovejectors of *Ashworthius sidemi* (Fig. 20), *A. tuyenquangi* (Fig. 22), and *A. lerouxi* (Fig. 23) were found to be closely similar to those of *Haemonchus* spp. The ovejectors of *A. patriciapilittae* (Fig. 21) differed from the other 3 *Ashworthius* spp. available for study and from all 12 *Haemonchus* spp. in lacking a distinct junction between the cylindrical part of the sphincter and the vestibule and in having a shorter ovejector overall. The cylindrical second part of the sphincter is represented by a tapering wedge of muscle fibers (in optical section) (Fig. 21) about equal in length to the adjacent, rounded, proximal part of the sphincter (Hoberg et al., 2002).

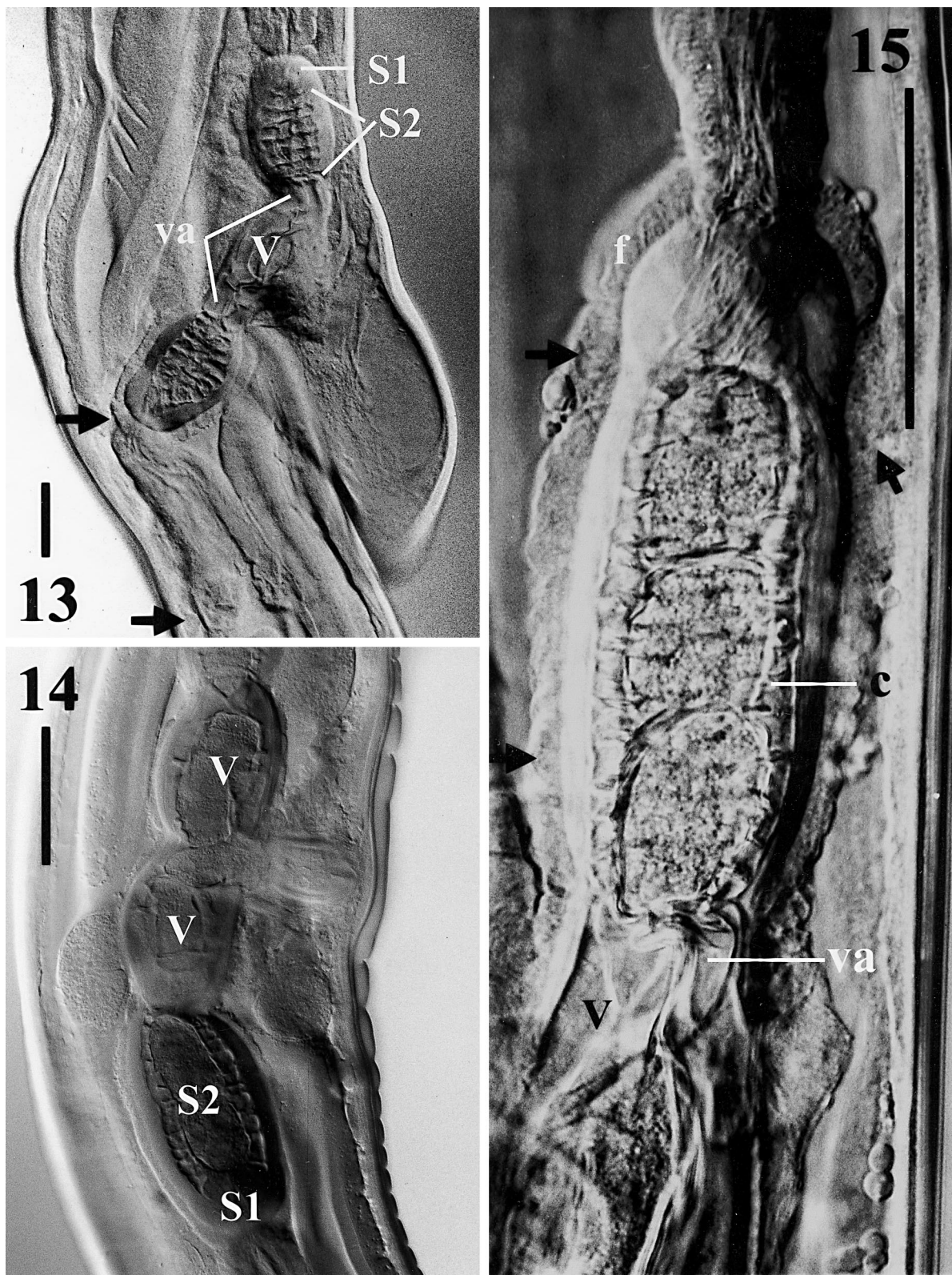
The ovejectors of *Mecistocirrus digitatus* were found to be similar to those of *Haemonchus* spp., with constrictions at the junctions of the 3 major parts of the ovejectors (Figs. 24, 25).

DISCUSSION

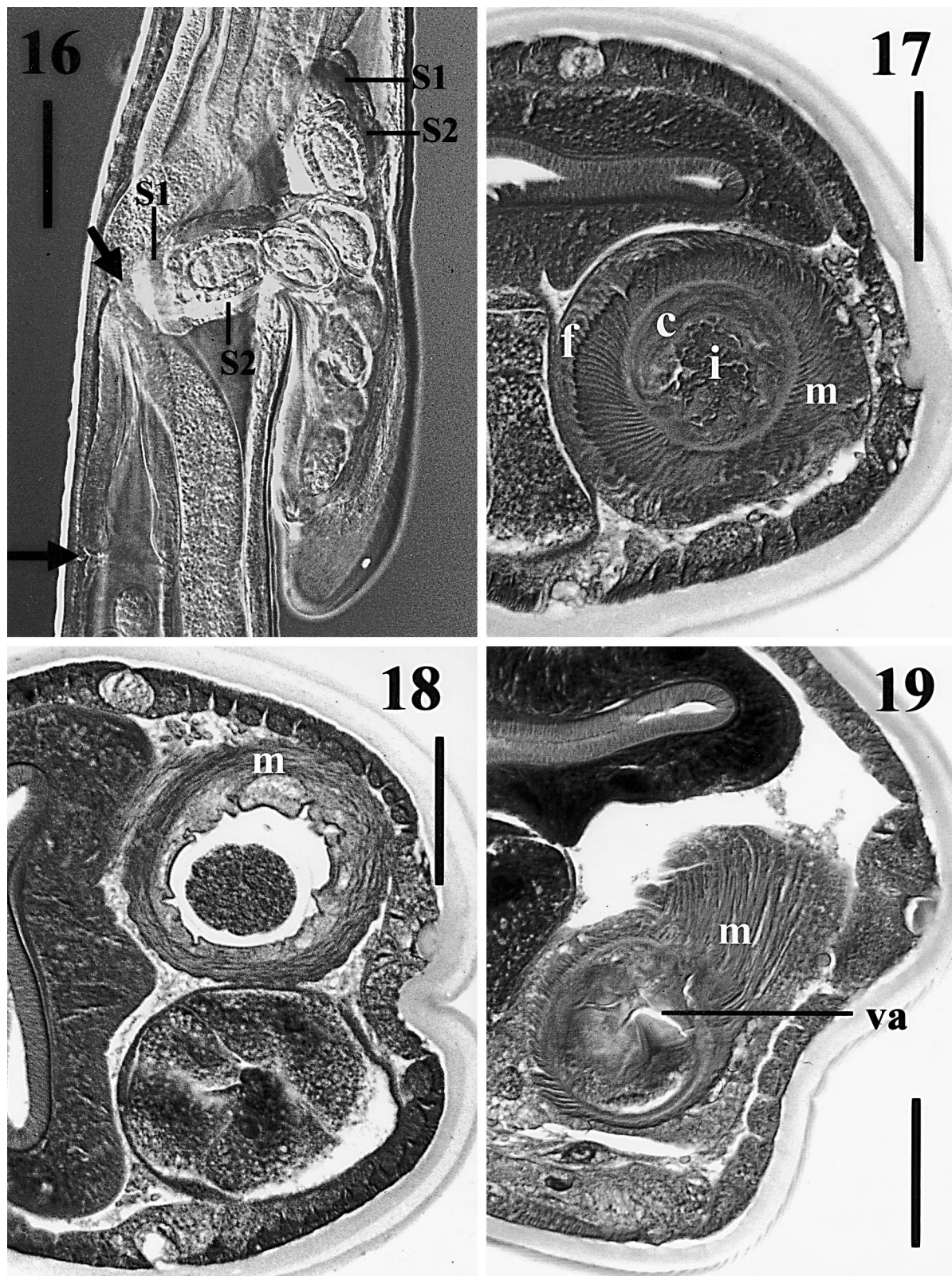
The terminology applied to ovejectors was reviewed by Chitwood and Chitwood (1950). In the classic redescrptions of



FIGURES 1–12. Drawings of ovejectors of *Haemonchus* spp., left lateral views. Bars = 200 μ m. **1.** Detailed drawing of ovejector of *H. placei* showing anterior infundibulum (i) with circular muscle fibers, anterior 2-part sphincter (S1 and S2) with spiral muscle fibers and a fluffy coat with 4 nuclei, vestibule (v) with thick cellular lining and ventral vagina, posterior sphincter with convoluted cellular lining, and posterior infundibulum with cellular lining with longitudinal ridging. **2–12.** Outline drawings showing shapes of parts of ovejectors (dashed lines mark slight constriction at junction of 2 parts of sphincters): **2.** *H. horaki*. **3.** *H. dinniki*. **4.** *H. lawrencei*. **5.** *H. contortus*. **6.** *H. krugeri*. **7.** *H. similis*. **8.** *H. mitchelli*. **9.** *H. okapiae*. **10.** *H. vegliai*. **11.** *H. longistipes*. **12.** *H. bedfordi*.



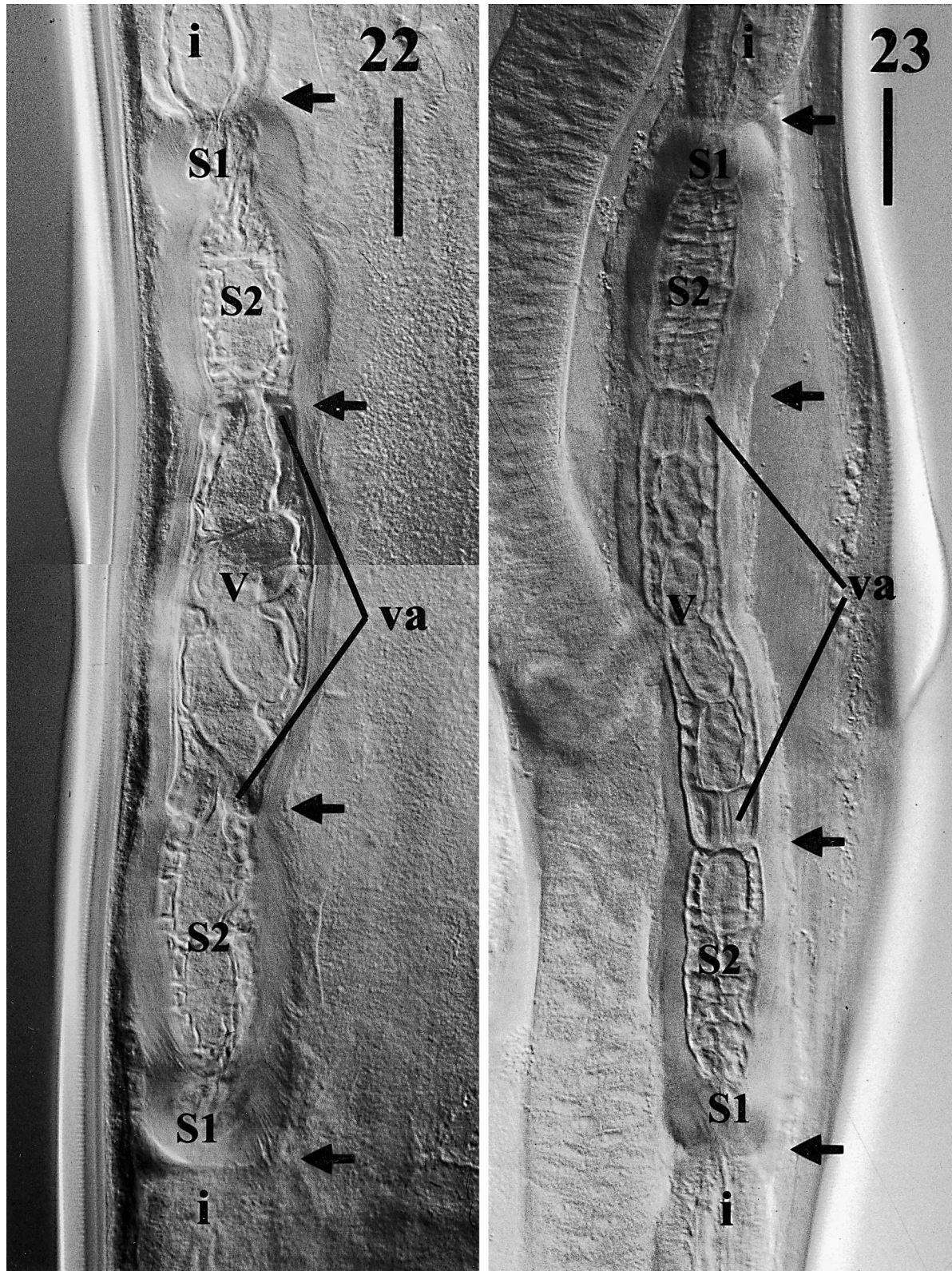
FIGURES 13–15. Ovejectors of *Haemonchus* spp., photomicrographs of cleared whole females, showing sphincters with thick proximal parts (S1), thinner-walled distal parts (S2) and a vestibule (V). Bars = 100 μ m. **13.** *Haemonchus dinniki* paratype showing anterior and posterior sphincters flanking the vestibule, with its lining cells forming valves at the junctions with the sphincter and the posterior infundibulum (between arrows). **14.** *Haemonchus lawrencei* syntype showing the posterior 2-part sphincter and the bipartite vestibule unique to this species. **15.** *Haemonchus contortus* showing the anterior 2-part sphincter covered by a fluffy coat (f) of sarcoplasm and nuclei (arrows) of muscle cells and lined by cells with a highly convoluted surface (c) and the anterior end of the vestibule lined with cells that at its proximal ends forms a valve (va).



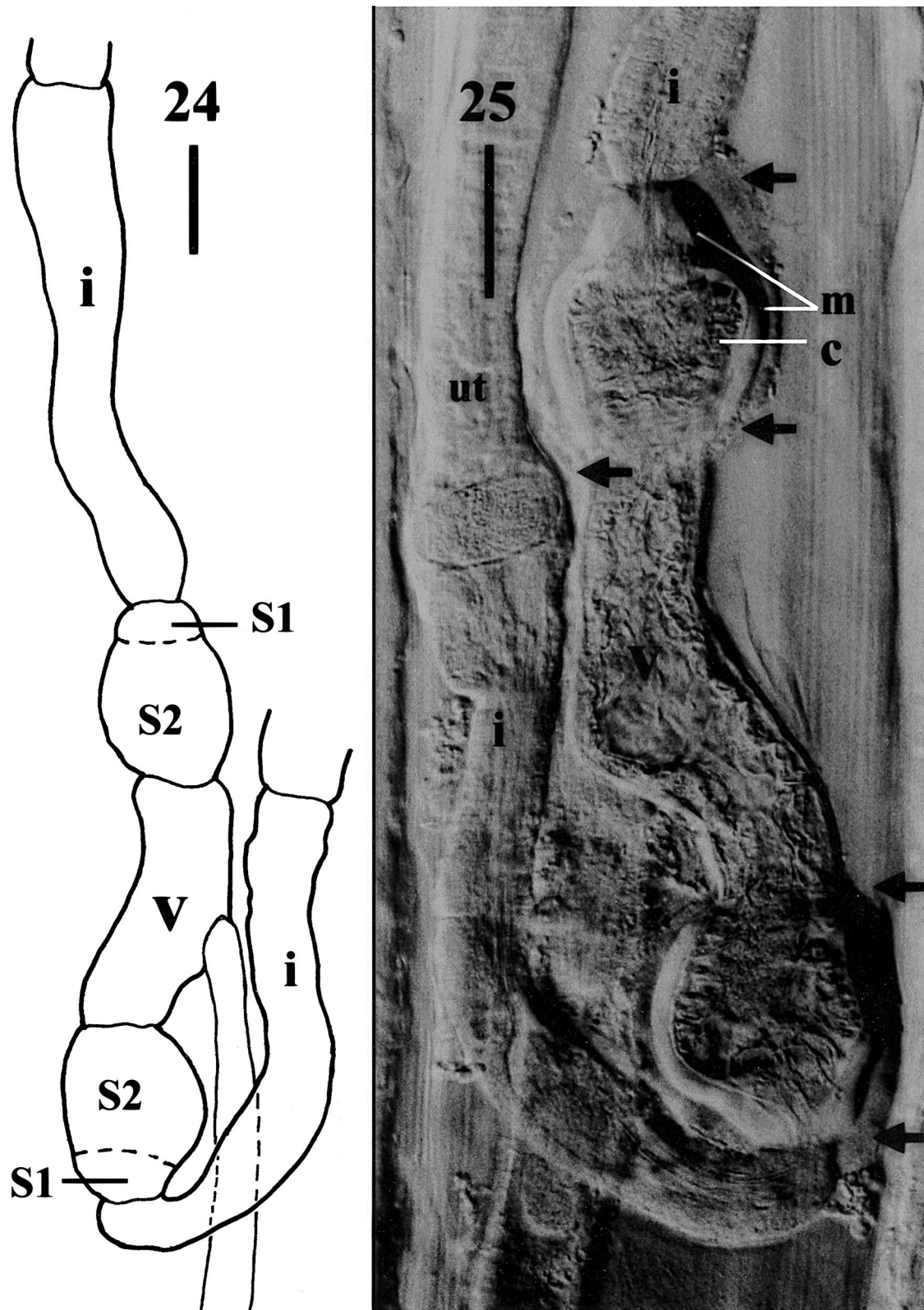
FIGURES 16–19. *Haemonchus similis*. **16.** Ovejectors in cleared, whole mount showing both 2-part sphincters (S1, S2) and posterior infundibulum (arrows), with vagina extending through vulvar lobe as is typical of this species. Bar = 100 μ m. **17.** Cross section through sphincter 1 showing its thick, spiral muscle fiber layer (m) and cellular lining (c) surrounding the base of the infundibulum (i) and the fluffy coat that covers it (f). Bar = 50 μ m. **18.** Cross section through proximal half of infundibulum showing circular muscle fibers (m) and the lining cells with ridges projecting slightly into the lumen that encloses a thin-shelled egg. Bar = 50 μ m. **19.** Cross section through junction of sphincter 2 and vestibule showing muscle fibers (m) of sphincter 2, which are almost parallel to its lumen at this point, and lining cells of the vestibule (va). Bar = 50 μ m.



FIGURES 20, 21. Ovejectors of *Ashworthius* spp. Photomicrographs of cleared specimens. Bars = 100 μ m. **20.** *Ashworthius sidemi*, showing anterior and posterior 2-part sphincters (S1, S2) with constrictions (arrows) at junctions with infundibula (i) and vestibule (V). **21.** *Ashworthius patriciapilittae*, showing 2-part sphincters (arrows) without constrictions at junctions with vestibule (middle arrows).



FIGURES 22, 23. Ovejectors of *Ashworthius* spp. Photomicrographs showing anterior and posterior 2-part sphincters (S1, S2) and internal cuticular valves (va) at proximal ends of vestibule (V). Arrows mark constrictions at junctions with infundibula (i). Bars = 100 μ m. 22. *Ashworthius tuyenquangi*. 23. *Ashworthius lerouxi*.



FIGURES 24, 25. Ovejectors of *Mecistocirrus digitatus* showing anterior and posterior 2-part sphincters (S1, S2), infundibula (i), and vestibule (V). Bars = 100 μ m. 24. Outline drawing showing shape and size of ovejector parts. 25. Photomicrograph showing thick muscle layer (m) of sphincter 1 and sphincter 2 and convoluted cellular lining (c) of sphincter 2. Arrows mark junctions of vestibule with sphincters, sphincters with infundibula, and posterior infundibulum with uterus (ut).

Haemonchus spp. by Ransom (1911), the ovejectors were described only generally and parts were not distinguished. The ovejectors of *H. contortus* were described, in exquisite detail, by Veglia (1915). The terminology applied in the current study to the ovejectors of 12 species of *Haemonchus*, 4 species of *Ashworthius* (Figs. 20–23), and the monospecific *Mecistocirrus* (Figs. 24, 25) follows the concept of Veglia (1915) and the terminology modifications of Chitwood and Chitwood (1950). Veglia recognized 3 sections of the ovejectors. He used the term “pars haustrix” for the long, slightly funnel-shaped section that communicates at its broad end with the uterus. The modern term for the pars haustrix is the universally adopted “infundibulum” (Chitwood and Chitwood, 1950). Veglia used the term “pars ejectrix” for the 2-part middle section of the ovejector of *H. contortus*. The proximal end (pars ejectrix 1), the round, sphincterlike part, surrounds the distal end of the infundibulum. Both the sphincterlike part and the cylindrical part (pars ejectrix 2) of the sphincter have a thick layer of muscle with spiraling continuous fibers (Veglia, 1915) that clearly define it as a single structure demarcated at both ends by constrictions and discontinuities in muscle bands and lining cells (Figs. 1, 15). Unfortunately, the only modern term used for the entire pars ejectrix is “sphincter” (Chitwood and Chitwood, 1950), and in some trichostrongyloid nematodes the cylindrical part (pars ejectrix 2) is reduced and the demarcation between it and the vestibule is not distinct. An example of this can be seen in *Ashworthius patriciapillitae* (Fig. 21), although in *A. sidemi* (Schulz, 1933; Ferte and Durette-Desset, 1989) (Fig. 20), *A. tuyenquangi* (Fig. 22), and *A. lerouxi* (Fig. 23), the separation of the second part of the sphincter and the vestibule is distinct, as in all species of *Haemonchus* (Figs. 1–16) and in *M. digitatus* (Figs. 22, 25).

Recent descriptions of ovejectors of *Haemonchus* spp. by Lichtenfels et al. (1994, 2001, 2002) have followed the concept of Veglia (1915) by describing and illustrating the distinctly defined parts of the ovejectors including an infundibulum, a 2-part sphincter, and a vestibule. However, in a redescription of *H. placei* (Place, 1893) by Giudici et al. (1999), although the parts of the ovejector were not described in the text, a drawing provided did not show a constriction marking the junction of the cylindrical portion of the sphincters and the vestibule. The illustration of the ovejector of *H. placei* by Giudici et al. (1999) conforms to the concept presented by Durette-Desset (1983), in which the sphincter consists of only the rounded portion that surrounds the base of the infundibulum, and the barrel-shaped portion of the sphincter (concept of Veglia, 1915) is included with the vestibule.

A similar dichotomy of concepts exists for the ovejectors of *Ashworthius* spp. In the type species of the genus, *Ashworthius pattoni* Le Roux, 1930, a drawing shows an elongate, 2-part sphincter with marked constrictions at its extremities. Similarly, the original description of *Ashworthius sidemi* Schulz, 1933 included a drawing showing a sphincter of 2 parts with constrictions at the junctions of sphincters and the vestibule. However, in a redescription of *A. sidemi*, Ferte and Durette-Desset's (1989) drawings showed the round, sphincterlike first part of the sphincter but did not show the cylindrical, second part of the sphincter to be delimited by a constriction from the vestibule, again conforming to a 1-part concept of the sphincter, but incorrectly indicating no distinction between the second part of the sphincter and the vestibule.

As in *Haemonchus* spp., inconsistencies in descriptions of ovejectors of *Ashworthius* spp. have been common. The original description of *A. lerouxi* included a drawing of the ovejectors showing a 2-part sphincter with constrictions at the junctions with the vestibule (Diaouré, 1964). In a revision of *Ashworthius*, however, the ovejectors of *A. lerouxi* were figured without constrictions at the junctions of the sphincters with the vestibule (Pike, 1969). Our study of female *A. lerouxi* found a very slight constriction but clearly discernable boundaries between the lining cells at the junctions of the elongate, 2-part sphincters with the vestibule (Fig. 23). In the description (Drózd, 1970) of *A. tuyenquangi*, drawings of the ovejectors showed a narrowing between the second part of the sphincters and the vestibule, but a single, combined measurement was given for the paired sphincters and the vestibule. When we studied specimens of *A. tuyenquangi*, we found the junction of sphincters with the vestibule to be marked poorly externally by a slight constriction but clearly marked internally by the valve formed by the cells lining the vestibule (Fig. 22).

In addition to the 4 species of *Ashworthius* examined in this study, we were able to determine ovejector structure from published accounts of *A. pattoni*. Le Roux (1930) illustrated marked constrictions at the junctions of elongate sphincters with the vestibule of *A. pattoni*. Drawings in the descriptions of *A. martinagliai* and *A. perrilli* did not show a constriction at the junctions of the sphincters and vestibule. Although these 2 species were not available for study, judging from the short, thick shape of the ovejectors (Ortlepp, 1935; Chauhan et al., 1972), we predict that the structure of the sphincters of those species may be as described for *A. patriciapillitae* (Fig. 21).

The structural form of the ovejector represented in *A. patriciapillitae*, in which the cylindrical part of the sphincter is short and the junctions of the sphincters and the vestibule are not distinct, is present also in some species of the Ostertagiinae and Cooperiinae but not in *Trichostrongylus* spp., which have distinctly 2-part sphincters. Although it is beyond the scope of this article, our unpublished observations indicate that 2-part sphincters can be observed among, or within, most taxa of the Trichostrongyloidea.

We have attempted to demonstrate that the inconsistent application of terminology to ovejectors of Haemonchinae presents a barrier to the use of ovejector structure in the systematics of these important nematodes and their relatives. In an effort to encourage the application of a uniform terminology to homologous parts of the ovejector, we propose the use of the terms “sphincter 1” for the rounded part and “sphincter 2” for the cylindrical part. It is hoped that clarification of the terminology for ovejectors of the Haemonchinae will provide a model for ovejectors of the rest of the Trichostrongyloidea.

Chitwood and Chitwood (1950) cautioned that for comparisons of diverse taxonomic groups, attempts to homologize parts of the ovejectors would lead to little of value because the ovejectors are often of different origin. However, within monophyletic groups such as the Haemonchinae (Hoberg and Lichtenfels, 1994) and the Trichostrongyloidea (sensu stricto, of Durette-Desset et al., 1999; Gouy de Bellocq et al., 2001) the recognition of homologous parts of ovejectors should be possible. For the information to be gained from the recognition of homologous parts to be useful, differences in the terminology need to be resolved.

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